

ORIBATIDS - A MITE BIODIVERSE (ACARINA)

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Oribatids are reviewed for scientists/managers assessing whether to incorporate this group into their biodiversity or biomonitoring studies in Australia. Oribatids usually feed on soil fungi, bacteria, decaying plant material or a combination of these. They inhabit the soil in virtually all terrestrial ecosystems. Their biodiversity largely results from heterogeneities that this environment can provide. There are about 50 families, 120 genera and 220 species described from Australia representing respectively about 25%, 10% and 3% of the World's oribatid fauna. The utility of available keys is discussed and 11 family level taxa are reviewed in terms of their potential contribution to biodiversity research. Scanning electron micrographs are used to illustrate some important morphological characters. □ *Acarina, Oribatida, biodiversity, biomonitoring, external morphology, Australian fauna.*

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Oribatid mites (Suborder Oribatida or Cryptosigmata) are a dominant component of ground litter and soils in virtually every habitat, with some reports of densities exceeding 100,000 per m² (Norton, 1985). Many species are associated with moss and fungi, and a varied arboreal fauna is now being recognised in Australia (Walter & Behan-Pelletier, 1993; Walter et al., 1994).

This paper is intended as a brief review of the group for scientists or managers assessing whether to incorporate oribatids into their biodiversity or biomonitoring studies. The biodiversity of oribatids is examined from different perspectives. The most useful keys and a selection of taxa which seem to have potential value in Australian biodiversity research are briefly discussed. Reference is made to the more instructive papers on biology and ecology, most of which, unfortunately, deal with the Northern Hemisphere fauna.

ORIBATID BIODIVERSITY - PERSPECTIVES

Ancestral oribatids probably evolved in the Lower Devonian as saprophages in the early, developing soils (Norton et al., 1988). Apart from relatively minor but multiple forays into arboreal and aquatic habitats (and the radiation of the Astigmata), their descendants have remained in or close to the soil, evolving to take advantage of niche opportunities that heterogeneities in this habitat provide. Today, as many as 80 or more species may occupy the same area of forest floor contributing significantly to the biodiversity of the ecosystem.

Oribatid biodiversity can be viewed from different perspectives depending on the aims of the research. Thus, if the contribution of oribatids to decomposition processes in soil is the focus of research, biodiversity from the functional perspective of feeding biology will be of prime interest.

Oribatids are usually microphytophages (feeding mainly on soil fungi), macrophytophages (feeding on decaying leaf or woody material) or panphytophages, feeding on both fungi and decaying plant material (Luxton, 1972, 1991; Norton, 1985, 1990). Some can swap food preferences depending on availability, or show opportunistic polyphagy by including nematodes in their diet. The most detailed analyses of oribatid biodiversity in terms of feeding biology are those of Schuster (1956) and Luxton (1972).

Oribatids are mostly particulate feeders producing faecal pellets. They thus contribute to soil structure and facilitate litter decomposition by increasing the surface area available for attack by micro-organisms.

Partly because of their eclectic feeding tastes, oribatid populations seem to be relatively stable compared with the more 'r-selected' Collembola and fungivorous Prostigmata whose reproduction appears to be more responsive to changes in fungus supply (Norton, 1985). This generalisation may not hold in all environments or species. For example, Kinnear (1993) demonstrated marked fluctuations in numbers of certain species in coastal habitats north of Perth. These may be due to seasonal fluctuations in moisture though more research is required to demonstrate this.

Oribatid biodiversity can also be viewed across ecosystem types, between habitats or from one microhabitat to another. Large differences in diversity can be expected between, say, arid and moist montane ecosystems where vicariance as well as ecosystem effects contribute to biodiversity. A significantly reduced difference in species turnover might be expected between adjacent rainforest and sclerophyll communities where differences in temperature, humidity, litter type and soil may be among the important parameters. Lee (1985b) has presented preliminary data on oribatid faunal differences across different habitat types, both natural and modified, in South Australia. In natural habitats, he found both increased abundance and species richness with increased rainfall; low species richness in cultivated sites though a few species were very abundant. His final report is in preparation (Lee, pers. comm.), its utility greatly increased by Lee's taxonomic studies (see references).

Small-scale habitat changes on the forest floor, from litter to lichen and moss to mushroom, have been related to changes in oribatid species composition (Aoki, 1967; Hammer, 1972; Wunderle, 1992) and hence contribute to oribatid biodiversity. More subtle changes in microhabitat preferences, for example within the litter layer, may result in patchy lateral distributions of individual species. Parameters including variation in moisture, litter depth and altitude have been implicated in spacial changes in biodiversity on a seemingly uniform forest floor (Mitchell, 1978; Walter, 1985). In an elegantly designed study, Anderson (1978) demonstrated significant correlations between mite diversity and vertical microhabitat diversity in the soil and litter profile. Walter & Norton (1984) studied sympatric congeners in pine litter soil. They hypothesised that the non-random separation in body size ranges, in one case involving four *Scheloribates* spp., enabled the congeners to use the resources of soil spaces of different sizes, perhaps reducing competition.

ORIBATIDS AND BIOMONITORING

Oribatids have been used in other countries for monitoring the effects of pollution, reclamation of mining sites, reafforestation, silvicultural practices, hazard reduction burning and other perturbations (see Marshall et al., 1987 for references). In Australia, Kinnear (1991) demonstrated a marked reduction in numbers of individuals in sites more affected by mining activities. For ex-

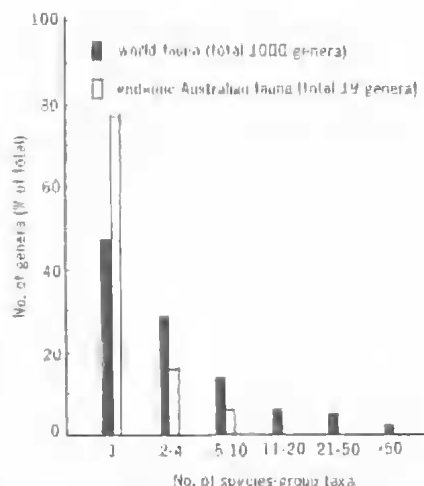


FIG. 1. Relative frequency of species-group taxa in World and 'endemic' Australian genera (World data adapted from Norton (1985)).

ample, sampled numbers of *Aphelacarus* sp. individuals varied from 34 to 264 on the three less disturbed sites and from 1 to 10 on the three more disturbed sites. Effects of burning have been studied in Australia by Moulton (1982) and Noble et al. (1989) with both studies attempting to identify to species level where practicable. Moulton defined two groups of oribatids in terms of their response to fire. Not unexpectedly, the group inhabiting surface layers was more seriously affected than the more euedaphic group. However, it would be interesting to know what 'trickle-down' effect frequent long term burning, an all-too-common practice in Australian forest management, has on deeper fauna.

Cranston (1990) lists seven criteria to assess suitability of taxa for biomonitoring. Oribatids perform strongly on most criteria: they are exposed to a variety of environmental parameters which affect the soil, they are functionally important in soil formation, they are ubiquitous, the numbers of species in a given locality are (probably) within manageable limits and have been shown to be responsive to certain environmental perturbations. However, their small size, difficulty in identifying many taxa to species level (and immaturity of our taxonomic knowledge), abundance of individuals often encountered, some difficulties in standardising sampling and extraction, and time taken in sorting are all negative aspects.

Difficulties with identification and numbers of individuals may be circumvented by the careful selection of 'priority taxa' which are more readily

recognisable but still representative of an important feeding guild or species assemblage. For example, *Otocepheidae* (below) warrant investigation as a potential representative group, at least for moister habitats.

IDENTIFICATION KEYS

A good place to start is with Norton's (1990) simplified and illustrated 'beginner's' key to family level taxa. Although intended for the North American fauna, the characters of value can quickly be appreciated and courage fortified before plunging deeper into the group. Norton's key can be supplemented by that of Moldenke & Fichter (1988) which contains useful SEM images and a glossary, as well as a general key to immatures. Luxton's (1985) comprehensive key to genus level for the New Zealand fauna is also useful as Australia has many taxa in common. Keys to several Australian taxa are given by Lee (see his papers referenced below for further citations). I am currently examining the feasibility of an Australian key for the non-specialist to family and where practicable to genus level, illustrated by SEMs as well as line-drawings.

In a recent key to World genera (Balogh & Balogh, 1992), Volume I contains keys and family lists, and Volume II ventral and dorsal illustrations of an exemplar from most genera. Apart from the illustrations which can frequently be used to arrive at a 'ball-park' family or genus, it suffers from some major disadvantages. It is not particularly 'user-friendly' and resort has to be made to Balogh & Mahunka (1983) for an explanation of terminology and zoogeographical abbreviations (latter not wholly consistent). There is no bibliography, though this gap can be filled in large part by Fujikawa (1991). Species numbers given for genera apparently include unpublished records.

The key also reflects a highly split, artificial classification with a plethora of monobasic taxa. As Norton (1985) points out, this type of classification may assist identification but can hinder, rather than advance, ecological and biogeographical generalisations based on an understanding of phylogeny. Unfortunately, their key ignores or overlooks some advances which have been made in our knowledge of higher level relationships. However, until there is a rival synthesis, Balogh and Balogh's key will continue to dominate oribatid classification.

	World fauna	Australian fauna	% of world fauna
No. of families	200	50	25
No. of genera	1000	100	10

TABLE 1. Relative numbers of described oribatid taxa in World and Australian faunas

OVERVIEW OF AUSTRALIA'S ORIBATID FAUNA

R.B. Halliday's 'Checklist and Bibliography' of Australian Acarina (Halliday, in prep) will be a valuable access point to the literature. He records approximately 50 families, 120 genera and 220 species from Australia, which represent respectively about 25%, 10% and 3% of the World's oribatid fauna (Table 1). In comparison, the North American fauna (Marshall et al., 1987) comprises about 120 families, 320 genera and 1200 species (respectively 60%, 27% and 16% of the World fauna). Of the Australian fauna, 1 family and 20 genera may at present be regarded as 'endemic', though 16 (80%) of these genera are monotypic (Fig. 1). These figures indicate the Australian fauna is poorly known particularly at the species level. Many other genera are represented in Australia (pers. obs.; D. C. Lee, pers. comm.) but have yet to be recorded in the published literature.

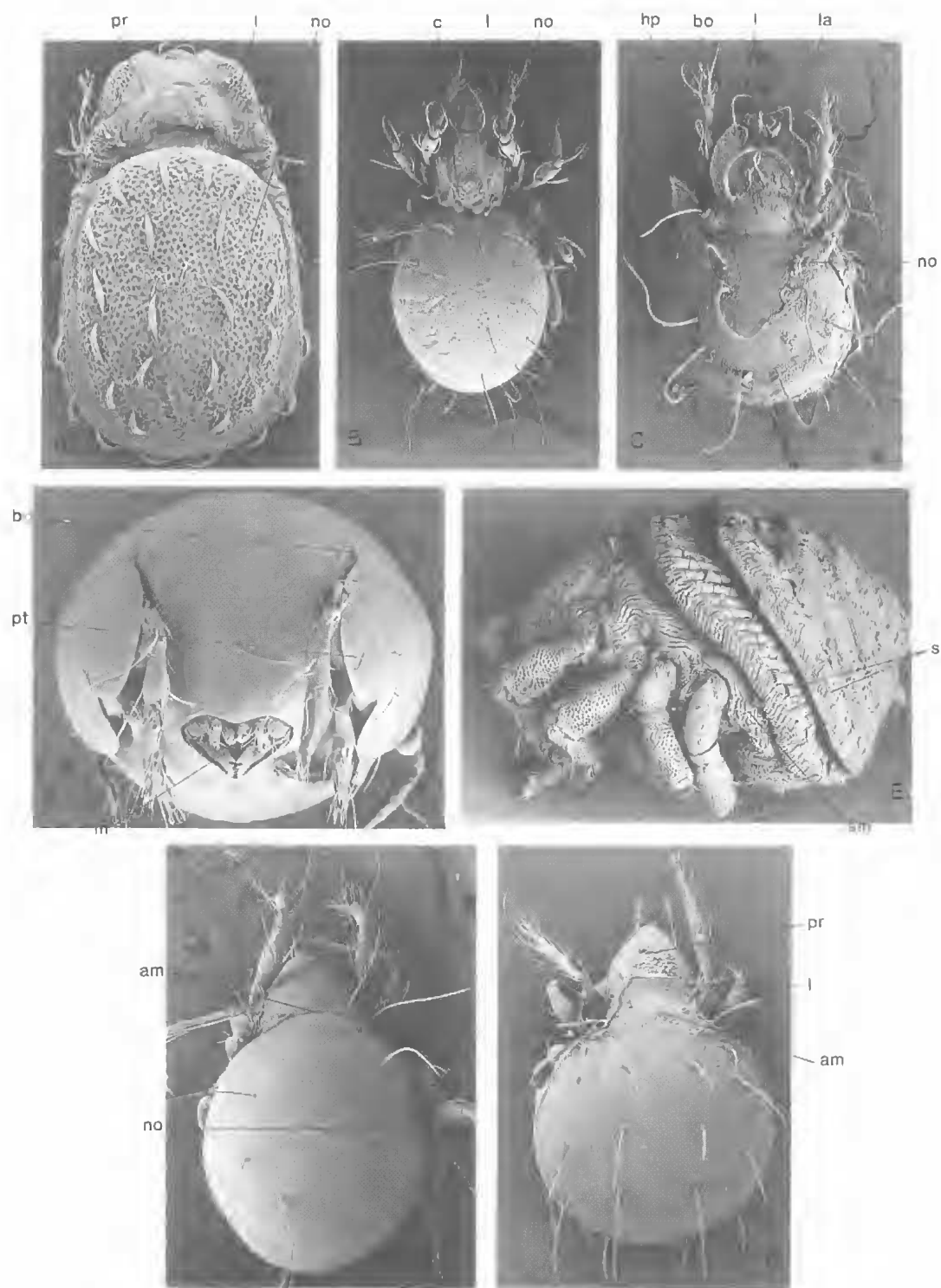
Some family level taxa appear to have more potential in biodiversity studies because they are more abundant, readily recognisable and/or better known at the species level. Other families are less 'user-friendly'. The following is a discussion of 11 family level taxa (citing of references not exhaustive).

Structures referred to in square brackets indicate some important characters labelled in the figures but are not necessarily diagnostic of each family.

(a) *Otocepheidae* (Fig. 2B). These are relatively large bodied, recognisable and among the more common mites in moister areas of Australia, especially *Pseudotocepheus* J. Balogh. A few species have been described by Balogh & Balogh (1983a, b).

(b) *Carabodidae* (Fig. 2A). Similar comments to the above apply, though these mites are not as plentiful in most samples. Some idea of range in variation is given by Balogh & Mahunka (1978).

(c) *Eutegaeidae* (Fig. 2C). These are similarly large and easily recognisable oribatids but tend to be less numerous in samples than the families



above. The superfamily Eutegaeoidea is reviewed by Luxton (1988) and keys given for families, genera and species.

(c) *Oppiidae* (Fig. 2F). These are among the most numerous and speciose oribatids in Australia but are also among the smallest and most difficult to identify. For example, a slide ostensibly of one oppiid morphospecies, proved to contain two families and three genera when examined by a specialist (D.C. Lee, pers. comm.). Perhaps a good, though narrow, introduction to the group and the type of systematic problems encountered is Lee & Subias (1991), who also list pertinent references to Australian species. Several Australian species originally placed in *Oppia* have been transferred to other genera as a search through Subias & Balogh (1989) reveals. Species are frequently lumped as 'Oppiidae' in ecological studies because of difficulty with identification.

(d) *Scheloribatidae* (not illustrated). This major group presents similar problems to the Oppiidae in terms of identification. An excellent grounding to the major genus in Australia, *Scheloribates* Berlese, is provided by Lee & Pajak (1990) (though Lee has developed a different setal nomenclature to that in common use). These authors report difficulty in separating infra- from interspecific variation but have found leg characters useful in delineating species. *Scheloribates* is widely distributed across a variety of Australian ecosystems and is an important intermediate host for tapeworms (Lee & Pajak, 1990).

(e) *Oribatulidae* (Fig. 2G). Like its closely related family above (d), some species occur in pasture, and may act as intermediate hosts for tapeworms (Roberts, 1953). About 15 species have been described from Australia with a sound foundation for the group established by Lee (1992). The 25 'oribatulid' species recorded by Lee (1985b) across different habitats in South Australia include some scheloribatid species (Lee, pers. comm.).

(f) *Phthiracaridae* (Fig. 3A). (including *Steganacaridae* of Niedbala, 1992). This is a group of 'box-mites' which is abundant in berlesates and which is featured on the 'Clunies Ross' side of Australia's \$50 note. Unfortunately, it and related families seem to be a grave-yard for many-a-misidentified taxon at the genus and species levels (see Niedbala, 1992). The single most important paper on the Australian fauna is Niedbala (1987). *Notophthiracarus* Ramsay is the most nominally speciose oribatid genus in Australia with 19 species described to date. The superfamily Phthiracaridae has been monographed on a world basis by Niedbala (1992) who discusses important characters and gives a generic level cladistic analysis. A major review of the Tasmanian fauna is in preparation (W. Niedbala & M. Colloff, pers. comm.).

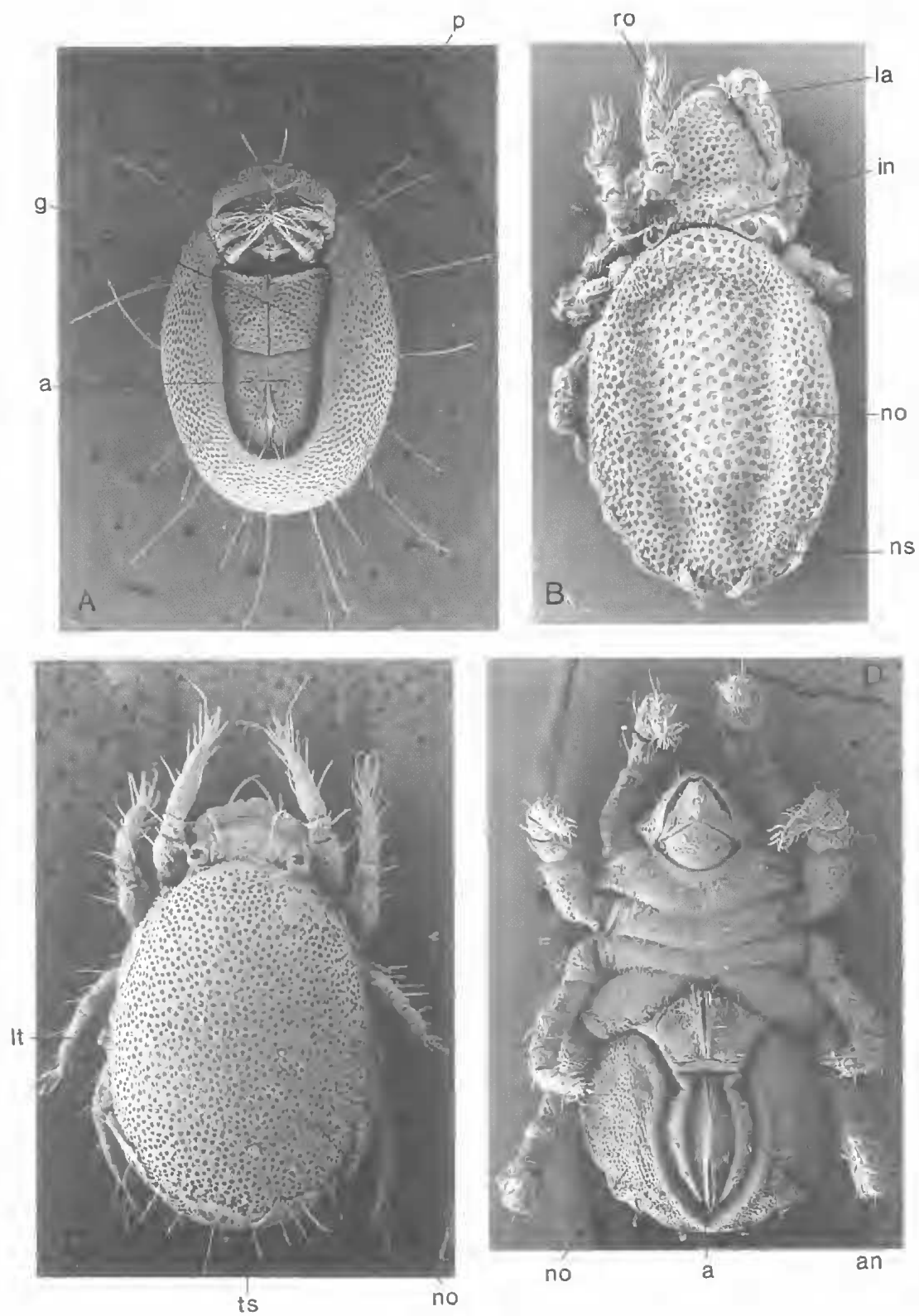
(g) *Galumnidae* (Fig. 2D). This is generally regarded as one of the most highly derived oribatid families in which various extensions of the exoskeleton enclose virtually all vulnerable parts. Although large bodied, a detailed study of setae and areas porosae is usually required to make species determinations. Balogh & Balogh (1983a) describe some species, while J. Stary of the Czech Republic (pers. comm.) is working on other elements of our fauna.

(h) *Pedrocortesellidae* (Fig. 3B). Although only four nominal species, all in *Pedrocortesella* Hammer, have been described (P. Balogh, 1985), this family and the closely allied Pheroliodidae have undergone major radiations in Australia, particularly in drier habitats. I am currently revising these groups.

(i) *Hermanniellidae* (Fig. 3C). Although not recorded in the Australian literature, this distinctive group is well represented in numbers of individuals, if not species, in many litter samples and appears to occur across a variety of ecosystems. *Hermanniella* Berlese is common in eastern Australian samples.

(j) *Brachychthoniidae* (not shown). This is one of the so-called 'primitive' or 'inferior' oribatid

FIG. 2. Variation in some oribatids. A = Carabodidae: no = notogaster oval, often heavily ornamented and with leaf-like setae; prodorsum broad, almost as wide as notogaster; l = lamella rounded, not blade-like. B = Otocephalidae: no = notogaster oval; c = condyles on prodorsum oppose condyles on notogaster; l = lamella narrow, almost a costula. C = Eutegaeidae: no = notogaster rounded; hp = humeral process or projection; bo = bothridium forming laterad expansion of prodorsum; l = lamella very large and blade-like; la = lamellar seta on cuspis. D = Galumnidae: pt = body with lateral wing-like flaps (pteromorphs) which are movable about a hinge and beneath which legs can retract, pteromorph extends anterior to bothridium; bo = bothridium; m = mouth-parts largely covered by extensions of cuticle (tecta). E = Liodidae: s = scalps (notogastral exuviae) of preadult instars; sm = body large and dark coloured, with striated margins. F = Oppiidae: no = notogaster globular and smooth; am = anterior margin of notogaster convex. G = Oribatulidae: am = anterior margin of notogaster not clearly delineated, notogaster fused with prodorsum; l = lamella narrow. Not to scale.



families. Some species are significant in drier habitats (Lee, 1985b; A. Kinnear, pers. comm.) but they are very small bodied. Some of the other primitive groups are covered by Lee (1985a) and his earlier work.

Many families not included in the above discussion may prove to be of considerable importance when the Australian fauna is better known. Some families and genera can be locally important. For example, *Liodes* sp. (Liodidae) (Fig. 2E), hitherto unrecorded in Australia, is quite common in the Brisbane area, while *Novonothrus* sp. (Nothridae) (Fig. 3D) is a dominant species in nearby Lamington National Park.

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LITERATURE CITED

- ANDERSON, J.M. 1978. Inter- and intra-habitat relationships between woodland Cryptostigmata species diversity and the diversity of soil and litter microhabitats. *Oecologia* (Berlin) 32: 341-348.
- AOKI, J. 1967. Microhabitats of oribatid mites on a forest floor. *Bulletin of the National Science Museum, Tokyo* 10(2): 133-138.
- BALOGH, J. & BALOGH, 1983a. New oribatid mites from Australia (Acari: Oribatei). *Acta zoologica Academiae Scientiarum Hungaricae* 29(1-3): 81-105.
- 1983b. Data to the oribatid fauna of Australia (Acari). II. *Acta zoologica Academiae Scientiarum Hungaricae* 29(4): 283-301.
1992. The oribatid mites genera of the world, Vols I & II. (Hungarian Natural History Museum: Budapest).
- BALOGH, J. & MAHUNKA, S. 1978. Data to the oribatid fauna of Australia (Acari). I. *Opuscula zoologica, Budapest* 15(1-2): 31-49.
1983. Primitive oribatids of the Palaearctic Region. (Series Eds: Balogh, J. & Mahunka, S. *The Soil Mites of the World*, I.) (Elsevier: Amsterdam).
- BALOGH, P. 1985. New oribatids from Australia (Oribatei). *Opuscula zoologica, Budapest* 19-20: 49-56.
- CRANSTON, P.S. 1990. Biomonitoring and invertebrate taxonomy. *Environmental Monitoring and Assessment* 14: 265-273.
- FUJIKAWA, T. 1991. List of oribatid families and genera of the World. *Edaphologia* 46: 1-130.
- HAMMER, M. 1972. Microhabitats of oribatid mites on a Danish woodland floor. *Pedobiologia* 12: 412-423.
- KINNEAR, A. 1991. Acarine communities of semi-arid soils from the Eastern Goldfields region of Western Australia. *Pedobiologia* 35: 273-283.
1993. Biodiversity of litter organisms: the impact of litter type. Abstracts, 'Towards Biodiversity and Conservation.' A Conference on Invertebrate Conservation and Biodiversity, Queensland Museum, Brisbane, 12-15 July 1993.
- LEE, D.C. 1985a. Sarcoptiformes (Acari) of South Australian soils. 4. Primitive oribatid mites (Cryptostigmata) with an extensive, unfissured hysteronotal shield and aplychoid. *Records of the South Australian Museum* 19(4): 39-67.
- 1985b. Mites of South Australian soils. Pp. 57-59. In Greenslade, P. & Majer, J.D. (eds), *Soil and Litter Invertebrates of Australian Mediterranean-type ecosystems*. WAITE School of Biology Bulletin 12, Adelaide.
1992. New species of Oribatulidae (Acarida: Cryptostigmata: Planofissuræ) from South Australian soils, with a review of subfamilies and Australian records. *Records of the South Australian Museum* 26: 37-49.
- LEE, D.C. & PAJAK, G.A. 1990. *Scheloriobates* Berlese and *Megascheloriobates* gen. nov. from southeastern Australia, with comments on Scheloriobatidae (Acarida: Cryptostigmata: Oripodoidea). *Invertebrate Taxonomy* 4: 205-246.
- LEE, D.C. & SUBIAS, L.S. 1991. *Bruchioppiella* species (Acari: Oribatida: Oppiidae) from South Australian soils. *Records of the South Australian Museum* 25(1): 19-30.

FIG. 3. Variation in some oribatids. A = Phthiracaridae: p = body form ptychoid, i.e. prodorsum can fold ventrad onto notogaster completely enclosing legs and gnathosoma; g and a = genital plates and anal plates broad, together forming large part of venter. B = Pedrocorresellidae: no = notogaster flatish or concave; la = lamellar seta mesad and anterior to rostral seta; ro = rostral seta; in = interlamellar seta minute; ns = notogastral setae restricted to posterior margin. C = Hermanniellidae: n = notogaster oval and convex, often punctate, shown here with tritonymphal scalp largely removed; lt = lateral tube carrying pore of hysterosomal gland; ts = remnant of tritonymphal scalp with its setae. D = Nothridae: no = notogaster wraps around to ventral side but does not fuse in ventral mid-line; a = anal plates; an = adanal plates not fused to anal plates. Not to scale.

- LUXTON, M. 1972. Studies on the oribatid mites of a Danish beech wood soil. *Pedobiologia* 12: 434-463.
1985. Cryptostigmata (Arachnida: Acari) - a concise review. Fauna of New Zealand. (Science Information Publishing Centre, DSIR: NZ), 106pp.
1988. A new mite superfamily (Acari: Cryptostigmata). *Zoological Journal of the Linnean Society* 93: 71-91.
1991. Seasonal and spatial variation in food intake by the oribatid mites of beech woodland soil. pp. 459-471. In Schuster, R. & Murphy, P.W. (eds), *The Acari, reproduction, development and life-history strategies*. (Chapman & Hall: London).
- MARSHALL, V.G., REEVES, R.M., & NORTON, R.A. 1987. Catalogue of the Oribatida (Acari) of continental United States and Canada. *Memoirs of the Entomological Society of Canada* 139: 1-418.
- MITCHELL, M.J. 1978. Vertical and horizontal distribution of oribatid mites in an aspen woodland soil. *Ecology* 59: 302-312.
- MOLDENKE, A.R. & FICHTER, B.L. 1988. Invertebrates of the H.J. Andrews Experimental Forest, Western Cascade Mountains, Oregon: IV. The oribatid mites (Acari: Cryptostigmata). United States Department of Agriculture Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-217: 112pp.
- MOULTON, T.P. 1982. The effect of prescribed burning and simulated burning on soil and litter arthropods in open forest at Cordeaux, N.S.W., Australia. (PhD Thesis, School of Biological Sciences, Macquarie University, Sydney).
- NIEDBALA, W. 1987. Phthiracaroida (Acari, Oribatida) nouveaux d'Australie. *Redia* 70: 301-375.
1992. Phthiracaroida (Acari, Oribatida) Systematic Studies. (Elsevier: Amsterdam).
- NOBLE, J.C., KALISZWESKI, M. & WHITFORD, W.G. 1989. Soil Acari from burnt and unburnt mallee habitats in western New South Wales pp. 224-225. In Noble, J.C., Joss, P.J. & Jones, G.K. (eds), *The mallee lands. A conservation perspective*, CSIRO: 224-225.
- NORTON, R.A. 1985. Aspects of the biology and systematics of soil arachnids, particularly saprophagous and mycophagous mites. *Quaestiones Entomologicae* 21: 523-524.
1990. Acarina: Oribatida. pp. 779-803. In D.L. Dindal (ed.) *Soil Biology Guide*. (John Wiley & Sons: Brisbane).
- NORTON, R.A., BONAMO, P.M., GRIERSON, J.D. & SHEAR, W.A. 1988. Oribatid mite fossils from a terrestrial Devonian deposit near Gilboa, New York State. *Journal of Paleontology* 62: 259-269.
- ROBERTS, F.H.S. 1953. *Zygoribatula longiporosa* Hammer (Oribatei: Acarina), an intermediate host of *Moniezia benedeni* (Moniez) (Anoplocephalidae: Cestoda) in Australia. *Australian Journal of Zoology* 1: 239-241.
- SCHUSTER, R., 1956. Der Anteil der Oribatiden an den Zersetzungsvorgängen im Boden. *Zeitschrift für Morphologie und Ökologie der Tiere* 45: 1-35.
- SUBIAS, L.S. & BALOGH, P. 1989. Identification keys to the genera of Oppiidae Grandjean, 1951 (Acari: Oribatei). *Acta zoologica Hungarica* 35(3-4): 355-412.
- WALTER, D.E. 1985. The effects of litter type and elevation on colonization of mixed coniferous litter bags by oribatid mites. *Pedobiologia* 28, 383-387.
- WALTER, D.E. & BEHAN-PELLETIER, V. 1993. Systematics and ecology of *Adhaesozetes polyphyllos* sp. nov. (Acari: Oribatida: Licneremaeoidea) leaf-inhabiting mites from Australian rainforests. *Canadian Journal of Zoology* 71: 1024-1040.
- WALTER, D.E., O'DOWD, D.J. & BARNES, V. 1994. The forgotten arthropods: foliar mites in the forest canopy. *Memoirs of the Queensland Museum* 36: 221-226.
- WALTER, D.E. & NORTON, R.A. 1984. Body size distribution in sympatric oribatid mites (Acari: Sarcoptiformes) from California pine litter. *Pedobiologia* 27: 99-106.
- WUNDERLE, I. 1992. Die Oribatiden-Gemeinschaften (Acari) der verschiedenen Habitate eines Buchenwaldes. *Carolinae* 50: 79-144.